

## Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species; an example from ants

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**Abstract** We collected ants from six urban and one forest land-use types in Raleigh, NC to examine the effects of urbanization on species richness and assemblage composition. Since urban areas are warmer (i.e., heat island effect) we also tested if cities were inhabited by species from warmer/drier environments. Species richness was lower in industrial areas relative to other urban and natural environments. There are two distinct ant assemblages; 1) areas with thick canopy cover, and 2) more disturbed open urban areas. Native ant assemblages in open environments have more southwestern (i.e., warmer/drier) distributions than forest assemblages. High native species richness suggests that urban environments may allow species to persist that are disappearing from natural habitat fragments. The subset of species adapted to warmer/drier environments indicates that urban areas may facilitate the

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movement of some species. This suggests that urban adapted ants may be particularly successful at tracking future climate change.

**Keywords** Urban heat island · Range shift · Ant diversity · Urban ecology

## Introduction

As global populations rise, many rural areas are experiencing human population declines due to migration to cities (Miller and Hobbs 2002; United Nations 2007). Most people now live in urban environments, the fastest growing environment globally (United Nations 2007). Therefore, the wildlife species most people encounter are species in urban environments (Dunn et al. 2006; Shochat et al. 2006). Species in urban environments can derive from the local “native” species pool, but also from non-native species (including invasive and pest species) from the global pool (Mack and Lonsdale 2001; McKinney 2006; Kark et al. 2007). To date, work aimed at understanding urban biomes has focused on the degradation or conservation of patches of “natural” environments and the organisms that persist in them (Bolger et al. 2000; McKinney 2006; Williams et al. 2009). Yet the less studied urban matrix of cement and lawns in which these “natural” patches reside represents one of the fastest growing biomes in the world (United Nations 2007). The origins of urban species and composition of urban faunas in both the “natural” and novel elements of urban landscapes is fundamental to understanding the biological world we most often experience.

Given the recognized importance of arthropods both in terms of ecosystem services and disservices and as a model system for other organisms (e.g., McIntyre 2009), studies of urban arthropod communities have been surprisingly rare and often limited in scope. Ants in particular are important because they respond rapidly to environmental change, represent a variety of trophic levels, are important ecosystem engineers, and are of major economic concern (Hölldobler and Wilson 1990; Hedges 1998; Holway et al. 2002; Underwood and Fisher 2006). Most studies on ants have focused on fragments of natural habitats in urban environments and the differences in species richness across urban to rural gradients, with often inconsistent patterns between cities (McKinney 2008; McIntyre 2009). For example, a number of studies of ants have shown decreases in species richness in urban environments (Pisarski and Czechowski 1978; Suarez et al. 1998; Malozemova and Malozemov 1999; Yamaguchi 2004; Lessard and Buddle 2005; Pacheco and Vasconcelos 2007; Thompson and McLachlan 2007; Clarke et al. 2008) though others have shown little to no difference (Carpintero et al. 2003; Gibb and Hochuli 2003; Forsys and Allen 2005; Vepsäläinen et al. 2008).

Few *a priori* predictions for species richness and structure of urban assemblages exist. General statements in the literature argue that a subset of “generalist” species, especially in arthropods, do well in urban environments (e.g., more cement, fewer trees, smaller patches of native and exotic plants) (McIntyre 2009). In ants, it has been reported that such species tend to be non-native, or behaviorally dominant species which are able to defend resources and displace other ants at local scales (Pisarski and Czechowski 1978; Malozemova and Malozemov 1999; Carpintero et al. 2003; Gibb and Hochuli 2003; Yamaguchi 2004; Holway and Suarez 2006; Vepsäläinen et al. 2008; Stringer et al. 2009). But, there are few empirical studies that support the hypothesis that generalist species do better than other species in urban environments (McKinney 2008; Lach et al. 2010). An important next step is to consider the traits of such favored urban species in more detail. It remains conceivable that the species that do well with urbanization are generalists in some regards, but also tend to possess specific traits that predispose them to urban success. For example, Lundholm and

Marlin (2006) have suggested that urban environments most closely approximate cliff or talus slope environments, and so species inhabiting cities often have origins in cliff-like habitats, even though such habitats are globally rare. Separately, in a review of this work, Gamble (2004) argued that some forest canopy species (e.g., some lichens and mosses on buildings) should succeed in some urban environments (Delgadillo and Cardenas 2000). A more inclusive version of the cliff-side hypothesis is that urban species should come from open or more exposed habitats, including but not exclusive to cliff-sides and forest canopies.

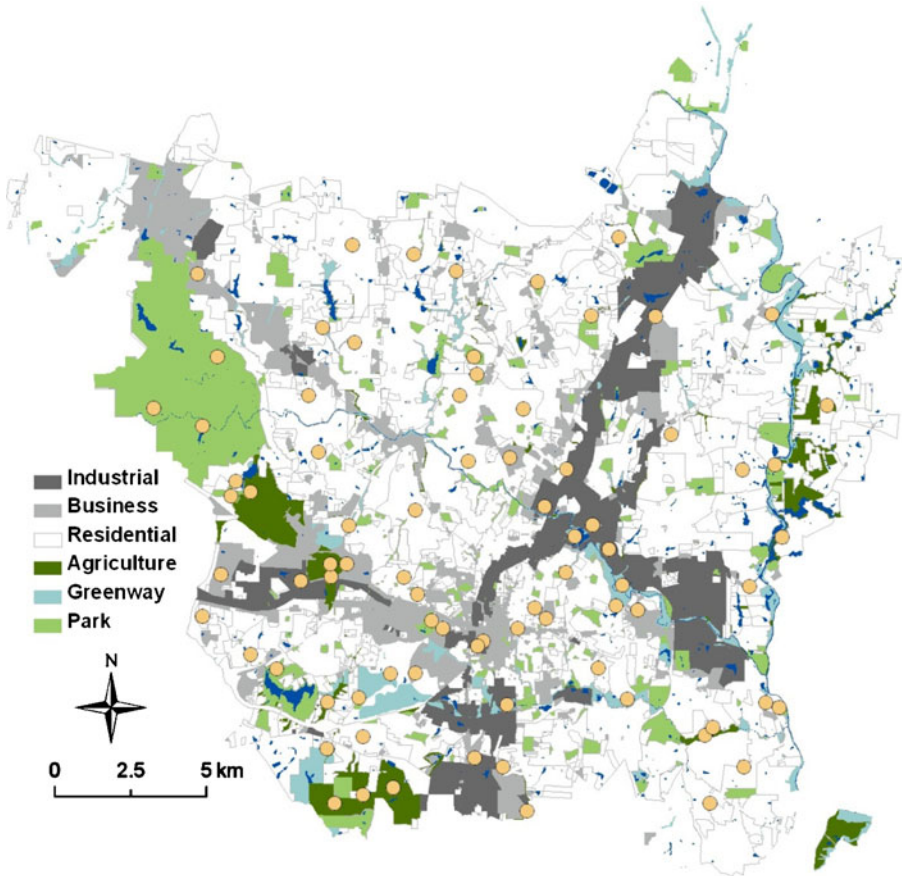
Urban environments also differ from surrounding natural areas in their climate due to the urban heat island effect (Grimm et al. 2008). Urban environments are warmer, especially in the evening, than adjacent non-urban areas, and this difference in temperatures is often greater than the predicted global temperature change (Grimm et al. 2008). Therefore, another though not exclusive possibility is that the species in the most open urban environments come disproportionately from species in warmer and drier environments (Bernard 1958; Pisarski and Czechowski 1978).

Here we address three broadly overlapping questions. While characterizing ant assemblages relative to different urban environments, we ask: 1) Does ant species richness decrease as a function of urbanization along a gradient of “natural” forest environments to intensive open urban areas?; 2) Do different urban environments support different ant assemblages?; and, 3) Does increasing urbanization favor a group of species found in warmer and drier natural environments (analogous to warmer/drier urban areas)? To address these questions we sampled ant assemblages from urban and natural areas in North Carolina, USA, and developed a database of the biogeographic and climatic traits of all ant species found along that gradient.

## Methods

### Study site and sampling

The city of Raleigh is located in northeast central North Carolina at the intersection of the Piedmont and Atlantic Coastal Plain biomes. North Carolina is a transition area where northern and southern faunas intersect (Carter 1962). As of the 2006 census, Raleigh was home to about 356,000 people and covered 299 km<sup>2</sup>. We used the Wake\_Zoning\_2006 GIS data-layer to quantify different urban land-use habitats (<http://www.wakegov.com>). City zoning classifications were broken into six urban land-use types: (ordered by percent coverage) agriculture (4.2%), greenway (4.4%), industrial (10.6%), business (11.1%), park (11.3%), and residential (58.3%). Coordinates for 10 sites were randomly selected for each land-use type except for residential in which 30 sites were randomly selected (Fig. 1). In addition, we sampled 10 natural forested sites from the surrounding area outside the city boundaries. Forested sites were upland hardwood or pine—hardwood mature secondary forests. All sites were randomly selected using Hawth's Tools for ArcGIS (Beyer 2004). Each site was sampled with five pitfall traps arranged in the shape of a 5 on a die separated by 20 m on a side. Pitfall traps consisted of 50 mL centrifuge tube filled with a water / alcohol / glycerol solution and left open for 5 days. All sampling occurred during 29 May–17 June 2008. All ants were identified to species and voucher specimens are deposited at the Bohart Museum of Entomology, University of California Davis (UCDC). Each species was assigned one of four categories (forest specialist, open specialist, generalist, or invasive) based on literature and expert knowledge.



**Fig. 1** Sample locations in Raleigh, North Carolina urban land-use types

#### Environmental data

Categorizing sites by land-use type (especially legal allowance) may not accurately describe the environmental characteristics of sites important to animal and plant assemblages (McIntyre et al. 2001). To account for variation in environmental characteristics within each land-use type we used satellite measures of five environmental variables: the Normalized Difference Vegetation Index (NDVI), percent canopy cover, percent impervious surface, radiant surface temperature, and the Normalized Difference Wetness Index (NDWI). Impervious surface and percent canopy cover were downloaded from Multi-Resolution Land Characteristics Consortium (<http://www.mrlc.gov/>) and were calculated from the 2001 National Landcover Database (Yang et al. 2002; Huang et al. 2003; Homer et al. 2004). NDVI (Rouse et al. 1973) and NDWI (Gao 1996) were calculated from geometrically and atmospherically corrected surface reflectance estimates retrieved from a Landsat-5 Thematic Mapper image acquired on 8 May 2005 (Sexton unpublished data), and at-satellite radiant temperature was calculated from the thermal band of the same image (Chander and Markham 2003). Similar to NDVI's use of red and Near-Infrared (NIR) reflectance to estimate photosynthetic potential, the NDWI uses the normalized difference between

shortwave-infrared (SWIR) and near-infrared to quantify canopy moisture content (Gao 1996):

$$\frac{NIR - SWIR}{NIR + SWIR}$$

NDWI has also been used to monitor water content in natural and agricultural herbaceous cover (Jackson et al. 2004; Gu et al. 2007).

To avoid errors due to local variation and spatial mis-registration between data sources, we collected average values of NDVI, NDWI, percent canopy cover, percent impervious surface, and radiant temperature within a 90-m circular window centered on each plot. Percent canopy cover and impervious surface were arcsine-square-root transformed prior to analysis. Principle Components Analysis (PCA) was performed using JMP 8.0 (SAS Institute, Cary, North Carolina, USA) on all five continuous variables, and the values from the first PCA axis were used as an index of environmental condition for each site.

*Hypothesis 1: Patterns in species richness* Species richness for each land-use type was determined by the total number of species pooled from pitfall traps at each site. Differences in ant species richness between urban land-use types was determined using a one-way ANOVA; all pair-wise comparisons were made with Tukey's multiple comparisons procedure to compare richness patterns among land-use types. In addition, a univariate regression model was performed using sample site scores from the first PCA axis to predict species richness in order to determine if there was a linear relationship between actual environmental characteristics and ant species richness. All statistics were performed using JMP 8.0 (SAS Institute, Cary, North Carolina, USA).

*Hypothesis 2: Assemblage composition* We first compared assemblage structure between sites by looking at the number of forest and open habitat specialist species at each site using univariate regression with the first PCA axis in JMP 8.0 (SAS Institute, Cary, North Carolina, USA). We then used Non-metric Multidimensional Scaling (NMS) using ant species abundances at each site to determine the distinctiveness of the ant assemblages in each land-use type. The abundance of each species was quantified at each site by the proportion of pitfall traps in which each species occurred. NMS was selected because it does not make assumptions about the shape of species' distributions or the relationships between species' occurrences and the underlying environmental gradients. NMS is based on pair-wise sample dissimilarities; for this analysis, we used Sorensen's (Bray-Curtis) similarity index to calculate species dissimilarity between all pairs of samples, then a Monte Carlo randomization to test the significance of the solution, and used the "thorough" option available in PC-Ord 4.0 (McCune and Mefford 1999), using a random starting configuration and 500 iterations. The stability criterion was a standard deviation in stress of less than 0.000001. We then used Multi-response Permutation Procedures (MRPP) based on Sorensen's (Bray Curtis) similarity index to test for differences in community structure between land-use groups. All pair-wise comparisons were performed to look for similarities between land-use groups. The MRPP was performed in PC-Ord 4.0 (McCune and Mefford 1999).

*Hypothesis 3: Warmer and drier adapted ants* The geographic range of each native ant species was extracted from the North American Database of Ant Species (<http://www.antmacroecology.org/projects.html>, M. Weiser *pers. com.*, also see Appendix 1). Using these distributions we extracted the maximum temperature and minimum precipitation experienced

by each native ant species in its range from WorldClim (Hijmans et al. 2005, see Appendix 1). We used two-way ANOVAs to test how urban land-use type, the number of ant species at a site, and their interaction influenced range distribution and environmental tolerance that occur at each site. We performed four separate two-way ANOVAs; the response variables were average minimum latitude (southern limit), minimum longitude (western limit), minimum precipitation (dry adapted), and maximum temperature (warm adapted) of all species present at each site. The interaction term was never significant and therefore is not presented in the results. Two sample t-tests were used to determine if open habit specialist species differed in their ranges or environmental tolerances from forest habitat specialist species. All statistics were performed using JMP 8.0 (SAS Institute, Cary, North Carolina, USA).

## Results

We captured 7,227 individual ants from 54 species in the urban environments and surrounding forests. Five are non-native species (Appendix 2). Species richness ranged from 2–16 across sites (mean  $\pm$  standard deviation =  $7.7 \pm 3.1$ ). The most diverse site was classified as agriculture, but had been allowed to regenerate to young secondary growth forest, whereas one agricultural, one industrial, and two residential sites only captured two species each. The seven most widespread species, listed by the proportion of sites occupied, were *Solenopsis molesta* (70%) a habitat generalist, *Pheidole dentata* (60%) an open habitat specialist, *Monomorium minimum* (54%) a habitat generalist and pest species, *Nylanderia* (formerly *Paratrechina*) *vividula* (43%) an open habitat specialist and pest species, *S. invicta* (42%) a widespread invasive species, *Formica subsericea* (37%) a forest habitat species, and *Aphaenogaster carolinensis* (35%) a forest habitat species.

The first axis of the PCA (hereafter PC-I) created using the five environmental variables (% canopy cover, % impervious surface, NDWI, NDVI, and radiant surface temperature) from each sampling site explained 84.1% of the variation between sites. The eigenvectors for % impervious surface and surface temperature were both  $-0.44$ , while NDVI, NDWI, and % canopy cover were  $0.46$ ,  $0.46$ , and  $0.44$  respectively. The one-way ANOVA of urban land-use habitats and the first PCA axis was significant ( $F_{6,82} = 18.70$ ,  $p < 0.0001$ , adj.  $r^2 = 0.55$ ) and resulted in three distinct groups; heavily urbanized (industrial & business), less disturbed (park & agriculture), and natural areas (greenway & forest) with residential being intermediate between heavily urbanized and less disturbed habitats (Table 1).

**Table 1** Mean ( $\pm$  SE) PCA axis 1 scores of urban land-use habitats. PCA scores are based on % impervious surface, radiant surface temperature, NDVI, NDWI, and % canopy cover

Habitat	Mean PCA axis 1 score	Standard error
Industrial	-2.96	0.26
Business	-1.94	0.49
Residential	-0.12	0.24
Park	0.70	0.65
Agriculture	0.82	0.50
Greenway	1.51	0.46
Forest	2.37	0.24

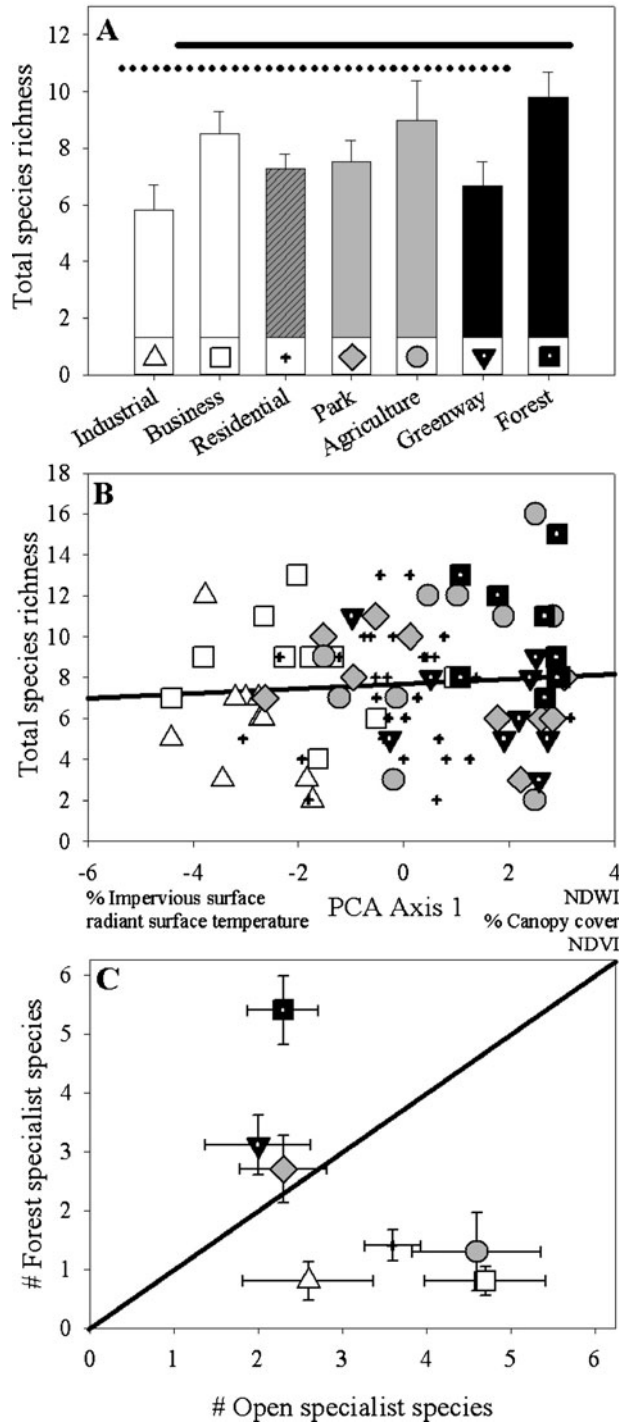
**Hypothesis 1: Patterns in species richness** There was a significant effect of land-use type on total species richness ( $F_{6,82}=2.29$ ,  $p=0.0427$ , adj.  $r^2=0.08$ ) at the landscape scale. In pair-wise comparisons however, the only difference was between forested and industrial sites, where industrial sites tended to have fewer species (Fig. 2a). Relative to PC-I (i.e., a continuous measure of urbanization), species richness did not vary predictably ( $F_{1,87}=0.51$ ,  $p=0.4761$ , adj.  $r^2=-0.01$ ) (Fig. 2b).

**Hypothesis 2: Assemblage composition** Although overall differences in species richness between sites or land-use types were subtle, the number of forest and open habitat specialist species that occurred in each land-use type were significantly different (Fig. 2c). Not surprisingly, sites with greater % canopy cover (i.e., less disturbed sites such as forests and greenways) had more forest specialists ( $F_{1,87}=20.40$ ,  $p<0.0001$ , adj.  $r^2=0.18$ ). Our data also suggests that open habitat specialist species may be more common in the same less disturbed areas ( $F_{1,87}=3.40$ ,  $p=0.0687$ , adj.  $r^2=0.03$ ). This counterintuitive pattern is explained by the observation that open areas with low percent canopy cover and which include the most urbanized environments (industrial areas) have the fewest species overall, whereas open but less disturbed areas (parks and agriculture) had some of the most diverse sites (Fig. 2). Forest and greenways had the fewest invasive and pest species per site (mean  $\pm$  standard deviation =  $1.7\pm 1.1$ ) while agriculture and business sites had the most invasive and pest species per site (mean  $\pm$  standard deviation =  $4.0\pm 1.4$ ). The most disturbed sites (industrial) have (mean  $\pm$  standard deviation =  $3.0\pm 1.7$ ) invasive species per site which continues the trend that industrial sites have fewer species than any other urban environment regardless of ant habitat preference or life history trait (Fig. 2).

NMS produced a three-dimensional solution with final stress 18.93 after 500 iteration runs (Fig. 3). On the first two axes, all forest and eight of the nine greenway sites cluster closely together in the lower-left corner. These sites correspond to where forest species such as several of the *Aphaenogaster*, *Crematogaster*, and *Camponotus* species were most abundant. The upper right corner of the first two axes was a cluster of the industrial and business sites. Residential, park, and agriculture sites were scattered throughout the figure without forming any distinct clusters. Forest sites were the only land-use zone to consistently cluster together on all three axes (Fig. 3). MRPP results confirmed that ant communities differed between habitats ( $T=-15.583$ ,  $A=0.117$ ,  $p<10^{-8}$ ). Pair-wise comparisons revealed that forest sites were the only sites to be distinct from all other land-use environments (Appendix 3).

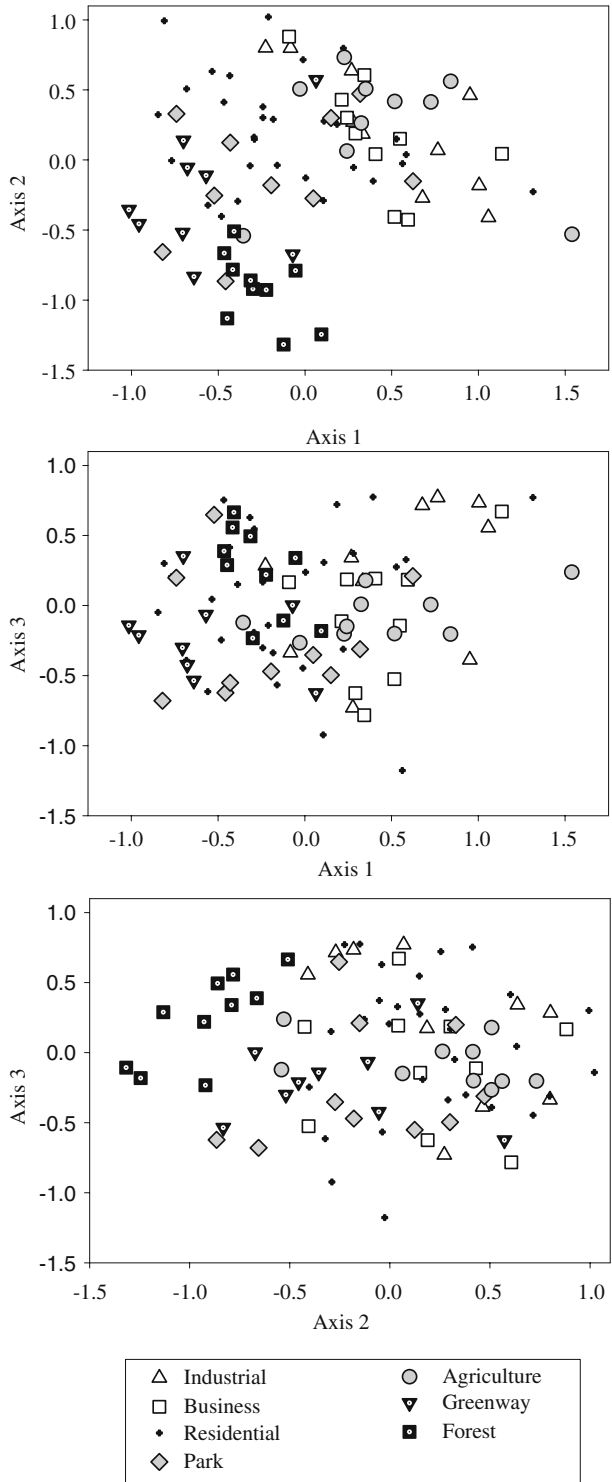
**Hypothesis 3: Drought and heat-adapted ants** Ant assemblages found in different urban land-use types represent non-random assemblies of ant species in North America (Fig. 3). Ant assemblages in more open and more urbanized sites (e.g., industry, business, agriculture) tended to be composed of species with distributions that extended both further south (two-way ANOVA minimum latitude: Habitat  $F_{13,75}=3.92$ ,  $p=0.0019$ , native species richness  $F_{13,75}=0.01$ ,  $p>0.05$ , adjusted  $R^2=0.21$ ) and west (two-way ANOVA minimum longitude: Habitat  $F_{13,75}=3.40$ ,  $p=0.0051$ ; native species richness  $F_{13,75}=12.53$ ,  $p=0.0007$ , adjusted  $R^2=0.34$ ) than ant assemblages in the natural more closed-canopied sites (Fig. 4a). Native species richness at a site was not important in determining the southern distribution of an assemblage, but did have an effect on the western distribution. As more species were found at a site, the average western extent of the site decreased. This difference in species distribution is also reflected in species tolerance to environmental conditions. Ant assemblages in more open and more urbanized habitats (e.g., industry, business, agriculture) tended to be composed of species which tolerated warmer (two-way ANOVA maximum

**Fig. 2** Patterns in total species richness across sites. **a** Differences in average ( $\pm$  SE) species richness by land-use category. Lines above the columns represent statistically similar groups. **b** Species richness at each of the 89 sample sites by their score on the first PCA axis. More negative values indicate greater % impervious surface and higher radiant surface temperatures, more positive values indicate higher NDVI, % canopy cover, and NDWI. **c** Average ( $\pm$  SE) number of native forest habitat and open habitat specialist species found in each urban land-use habitat. Solid line represents equal numbers of forest and open habitat specialist species. Generalist and invasive species are not included. Colors represent the four primary groupings of land-use zones indicated by an ANOVA using the first PCA axis

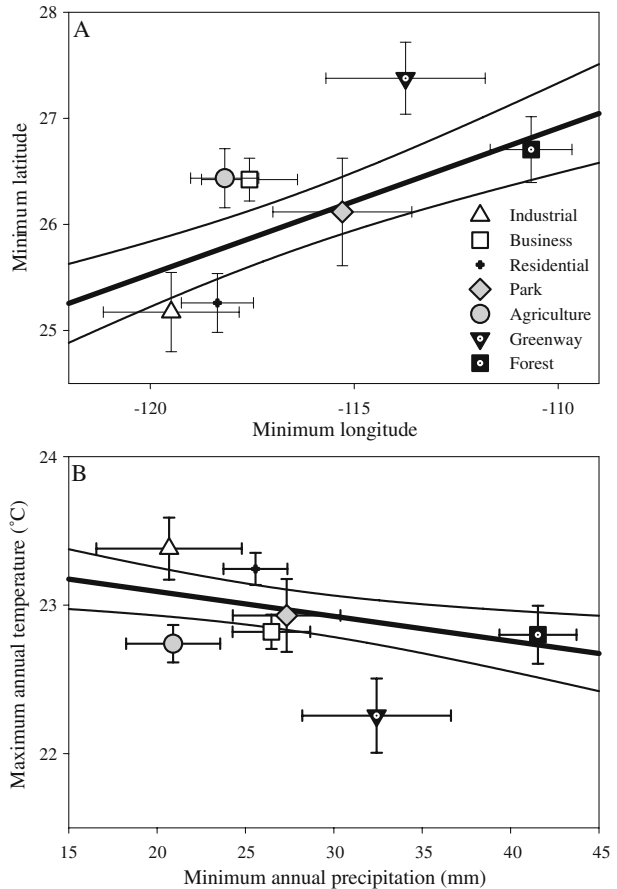




**Fig. 3** Three-dimensional Non-metric Multidimensional Scaling (Bray-Curtis distance matrix) for all 89 ant collection localities with final stress of 18.93. Symbols correspond to urban land-use zones. Colors correspond to groupings based on habitat characteristics from first axis of the PCA. All combinations of the three NMS dimensions are shown



**Fig. 4** Average species range distribution data by urban land-use habitats. **a** is the average ( $\pm$  SE) minimum longitude (western most occurrence) by minimum latitude (southern most occurrence) of the native ant assemblages in each site. Linear regression with 95% confidence interval fitted through all 89 sites ( $y=42.06+0.14x$ , Adjusted  $R^2=0.24$ ,  $F_{1,87}=29.47$ ,  $p<0.0001$ ). **b** is the minimum annual precipitation (mm) by maximum annual temperature ( $^{\circ}\text{C}$ ) experienced by each native ant species averaged ( $\pm$  SE) over the whole assemblage at each site by land-use habitat. Linear regression with 95% confidence interval fitted through all 89 sites ( $y=23.42-0.02x$ , Adjusted  $R^2=0.07$ ,  $F_{1,87}=7.41$ ,  $p=0.0078$ )



temperature: Habitat  $F_{13,75}=3.14$ ,  $p=0.0084$ ; native species richness  $F_{13,75}=2.14$ ,  $p>0.05$ , adjusted  $R^2=0.24$ ) and drier conditions (two-way ANOVA minimum precipitation: Habitat  $F_{13,75}=3.76$ ,  $p=0.0025$ ; native species richness  $F_{13,75}=12.63$ ,  $p=0.0007$ , adjusted  $R^2=0.34$ ) than ant assemblages in the natural more close canopied habitats (Fig. 4b). Differences in distribution and environmental tolerance were not caused by differences in the number of open- and forest-habitat species at each site because habitat specialists have similar distributions (minimum latitude:  $t\text{-test}_{35,6}=-1.70$ ,  $p>0.05$ , minimum longitude:  $t\text{-test}_{29,8}=-1.06$ ,  $p>0.05$ ) and environmental tolerances (maximum temperature:  $t\text{-test}_{35,7}=0.64$ ,  $p>0.05$ , minimum precipitation:  $t\text{-test}_{34,6}=-0.45$ ,  $p>0.05$ ). Ant species that are found in more heavily disturbed sites like industrial and business land-use types, on average, occur in areas of North America that experience drier (10–20 mm) and warmer ( $0.5\text{--}1^{\circ}\text{C}$ ) conditions than ant species found in forested sites (Fig. 4b). However, most of the variation in the environmental tolerances of species found in different sites cannot be explained by site-specific environmental characteristics or habitat type. Site-specific radiant temperatures and NDWI were uninformative predictors of patterns in assemblage tolerance to warm temperatures ( $F_{2,86}=2.11$ ,  $p>0.05$ ) and only moderately useful at explaining patterns of assemblage tolerance to dry conditions ( $F_{2,86}=7.40$ ,  $p=0.0011$ , adjusted  $R^2=0.13$ ).

## Discussion

### Summary

In our study, we addressed three main hypotheses in urban ecology; 1) impoverishment of species richness in urban environments relative to natural habitats, 2) biotic homogenization within urban environments, and 3) similarity among species inhabiting urban environments. We demonstrate that in Raleigh, NC species richness does not differ between urban land-use types based on city zoning ordinances. Surrounding natural forests are not more diverse than most urban environments (other than industrial sites, see Fig. 2a). While species richness does not differ dramatically between land-use types, assemblage composition does (Figs. 2c & 3). Most of the common species in the heavily urbanized areas have more southwestern distributions and, as a consequence, greater tolerance to dry conditions and warmer temperatures than species found in more natural forested sites. Importantly, these are the same conditions predicted to be favored in at least some models of global warming in the southeastern U.S. (IPCC 2007).

*Hypothesis 1: Patterns in species richness* Most studies of ant species richness patterns in urban environments have focused on natural fragments and paid less attention to the urban matrix (Suarez et al. 1998; Yamaguchi 2004; Thompson and McLachlan 2007; Clarke et al. 2008). Typically, studies of animals have found fewer species in urban areas compared to nearby natural environments, though the opposite pattern has been observed for plants (Grimm et al. 2008; McKinney 2008). One caveat is that very large parks within the urban matrix often exhibit species richness similar to natural environments (Bolger et al. 2000).

Our study is relatively unique in that we focused on the full spectrum of urban land-use types, rather than presuming all urban areas are the same (but see Vepsäläinen et al. 2008). Consequently, our results expand upon and may contradict previous findings. The only urban environments in our study with significantly fewer species than natural forests were heavily urbanized industrial areas (Fig. 2a), which have the greatest coverage of impervious surface, highest temperatures, and lowest percent canopy cover, NDVI, and NDWI (Table 1). Interestingly, site level characteristics alone were not a significant predictor of species richness (Fig. 2b), suggesting that urban land-use types or landscape characteristics are capturing some information missing from the environmental variables collected at each site (Minor and Urban 2010). Our results are similar to the findings of Minor and Urban (2010) who reported that the number of bird species in the same study area in North Carolina did not differ across the urban gradient. This pattern of similar species richness in urban and natural environments has also been reported in other studies that widely sampled different urban environments (McIntyre et al. 2001; McKinney 2008), whereas studies that focus on natural habitat islands in the urban matrix often find decreased levels of diversity (Lessard and Buddle 2005; Holway and Suarez 2006; Clarke et al. 2008). Perhaps the novel urban environments that cover large areas (such as residential zones) allow species to persist that are disappearing from smaller fragments of natural habitat.

*Hypothesis 2: Assemblage composition* Even though species richness did not differ dramatically between environments or sites (Fig. 2), composition did. We identified two distinct ant assemblages spanning the urban and natural sites (Fig. 3). Sites with a high percentage of canopy (forest, greenway, and park) tended to have large numbers of forest specialist species and also tended to be the areas covering the smallest spatial extent

(greenway and park areas account for 15.7% of urban area). In contrast, sites with less canopy cover (agriculture, business, industry, residential) tended to have more open habitat specialists (Fig. 2c). Counter to predictions from the literature (Carpintero et al. 2003; Vepsäläinen et al. 2008), the differences in assemblages were not driven by a replacement of native species by invasive species or of natural habitat specialists by urban habitat specialists. Of the three most common invasive species in our study, the pavement ant (*Tetramorium caespitum*) is an urban specialist (Hedges 1998), *Solenopsis invicta* is an open habitat / disturbance specialist (Tschinkel 2006) which is abundant in any area with lower levels of canopy cover, and *Brachyponera* (= *Pachycondyla*) *chinensis* is a forest habitat specialist and is most common in areas with high levels of canopy cover (*Pers. obs.*). Native, urban pest species such as *Tapinoma sessile*, *Monomorium minimum*, and *Nylanderia sp.* tended to be habitat generalists found in both open and forested environments (Lynch 1981; Menke et al. 2010) and were not drivers of the assemblage patterns we found. Perhaps most interesting is that residential areas (the most spatially expansive urban habitat type) varied greatly in their composition. They included sites that had ant assemblages very similar to those in undisturbed forest sites and also sites with ant assemblages similar to those in the most heavily disturbed industrial areas (Fig. 3, Appendix 3). These results beg the question of what traits are shared by species that tend to be found in the most open and disturbed urban sites. In other words, if the species in these are to be recognized in some way as “urban adapters,” what exactly is the adaptation?

*Hypothesis 3: Drought and heat-adapted ants* We found that the urban-adapted assemblages draw disproportionately from species with biogeographic distributions that differ from those found in native forests (Fig. 4a). These species tend to have ranges that extend into southwestern North America, areas with both drier and warmer climates (Fig. 4b). The industrial sites, for example, tended to include a nested subset of those species that can be found in Riparian habitats in the Chihuahuan Desert (Whitham et al. 2006). This result suggests a different suite of life history characteristics to focus on, in particular those associated with adaptations to living in more desert or scrub habitat conditions. Tolerance of extreme environments has also been linked to the success in urban environments of native plant species that are adapted to cliff-side habitats (Lundholm and Marlin 2006). The relatively low levels of variance in environmental tolerance or distribution explained by site level environmental characteristics (< 15%) compared to land-use habitats (24–34%) suggests that some other life-history traits must also be important. Previous work on ant species in urbanized environments has suggested that traits such as colony structure (Pacheco and Vasconcelos 2007; Cremer et al. 2008; Menke et al. 2010), behavioral dominance (Carpintero et al. 2003; Lessard and Buddle 2005), nest site preference (Vepsäläinen et al. 2008; Friedrich and Philpott 2009), or foraging guild/ecosystem service are also important traits (Gibb and Hochuli 2003; Thompson and McLachlan 2007; Sanford et al. 2009). All of these characteristics of species may help explain some of the variation in our study. It would be interesting to study these traits in such a way that also included the biogeographic regions where the species originated. Our work indicates that species with tolerance of climatic extremes may be favored in urban habitats more generally.

We see at least two possible mechanisms for the pattern observed in the biogeographic distribution of urban species. Perhaps the simplest explanation is that the hotter and drier conditions in heavily urbanized sites favor species from hotter and drier regions (Bernard 1958; Pisarski and Czechowski 1978). If this is the case, our results may generalize to many cities and additional taxa. A second and non-exclusive possibility is that characteristics of

urban areas favor soil nesting species rather than cavity nesters as suggested by Friedrich and Philpott (2009) or species that nest in rotten wood (Vepsäläinen et al. 2008). If this is true, we expect our results to be constrained to cities where the nearest habitat favoring soil nesting ants happens to be hotter and drier, like Raleigh NC. Other non-exclusive mechanisms also exist, but clearly the attributes of the species found in the most intensely urbanized sites that allow them to succeed both in such sites and in warmer and drier habitats deserve further study.

## Conclusions

A common assumption is that the expansion of urban environments will result in a faunal homogenization, driven mostly by the loss of native species and the differential success and human mediated transport of a few widespread generalist and invasive species (McKinney 2006). Vepsäläinen et al. (2008) find no evidence for such a pattern in their comparison of studies in ants across northern Europe. By the same token, our results suggest that diverse assemblages of native ant species are able to persist within a single urban area. Only four species were exclusive to natural forests (*Crematogaster vermiculata*, *Pyramica ornata*, *Temnothorax longispinosus*, and *T. texanus*). Species such as *Crematogaster vermiculata*, that nest under rotting logs may be nest site limited (Vepsäläinen et al. 2008), and the others are leaf-litter specialists which rarely fall into pitfall traps. All active terrestrial foraging forest species were also found in urban environments.

One reason ants may deviate from the expectation of faunal homogenization is the spatial scale at which they live. Like most invertebrates, and unlike most vertebrates (on which most urban animal studies are based), many ant colonies exist and experience the environment over a relatively small spatial extent (Yasuda and Koike 2009). To an ant colony in a single acorn, a hedgerow in a wooded yard may not be functionally different from a shrub in a forest. Similarly, we often find small leaf litter/rotten wood nesting ant species (i.e., *Strumigenys louisianae*, and *Pyramica spp.*) in mulch piles around trees in heavily urbanized areas (unpublished data). This overlap in species occurrence between natural and urban sites suggests that a model of the urban matrix isolating natural habitat islands due to dispersal limitations (Pacheco and Vasconcelos 2007) often used to describe diversity patterns of larger-bodied taxa may not be useful for ants and other small bodied taxa. For such taxa, the urban matrix may instead act as a corridor for dispersal at a spatial grain smaller than the focus of much of ecology.

A large number of native ant species appear to be able to persist in urban environments. These species have traits that may predispose them to success in both urban heat islands, and more generally, with climate change scenarios that predict both warming and drying (Williams and Jackson 2007; Williams et al. 2007). Cities may, in general, filter species' spatial responses to climate change, potentially acting as a corridor and accelerating the range shifts of some species pre-adapted to the urban landscape while slowing that of others. These species that are pre-adapted to the urban environment appear to be a diverse native assemblage of ant species which is important for maintaining ecosystem services (Lach et al. 2010).

Urban areas are often thought of as obstacles to native species' responses to global change (Mack et al. 2000; McKinney 2008). However, our results suggest the hypothesis that the urban heat island effect, which is often  $\geq +5^\circ\text{C}$ , may have already facilitated movement of species, and that the urban matrix may act as a corridor for the continued expansion of both native and non-native species. Examples of species that may have already moved due to the effects of heat islands include mammals (Kanda et al. 2009a;

Kanda et al. 2009b), birds (Chamberlain et al. 2009), and plants (LaSorte et al. 2008; McKinney 2008). These results suggest a broader principle, namely that those species that are able to succeed in urban environments may be proportionally more successful at moving with further human expansion and at tracking future climate change. Regardless, the lack of existing studies on the movement of native species within and across urban environments and the ability of urban areas to act as corridors for future expansion must be addressed.

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## Appendix 1

**Table 2** Southern and western distributional extents of native ant species based on the North American Database of Ant Species (<http://www.antmacroecology.org/projects.html>). Maximum temperature and minimum precipitation were extracted from WorldClim data based on the species range

Subfamily	Species	Minimum latitude	Minimum longitude	Maximum temperature (°C)	Minimum precipitation (mm)
Amblyoponinae	<i>Amblyopone pallipes</i>	27.250	-123.083	22.4	12.4
Dolichoderinae	<i>Dorymyrmex bureni</i>	27.250	-82.583	22.9	118.9
	<i>Forelius pruinosus</i>	10.750	-119.750	25.7	9.6
	<i>Tapinoma sessile</i>	20.250	-136.583	22.4	11.2
Ecitoninae	<i>Neivamyrmex texanus</i>	20.083	-113.583	22.5	12.2
Formicinae	<i>Brachymyrmex depilis</i>	26.750	-125.083	22.4	22.1
	<i>Camponotus americanus</i>	24.583	-120.417	24.9	32
	<i>Camponotus castaneus</i>	27.083	-100.083	22.6	64.7
	<i>Camponotus chromaiodes</i>	32.250	-95.750	17.8	82.3
	<i>Camponotus nearcticus</i>	26.083	-126.583	23.7	27.3
	<i>Camponotus pennsylvanicus</i>	28.750	-106.417	21.3	28.9
	<i>Formica dolosa</i>	28.770	-97.780	21.5	80.5
	<i>Formica subsericea</i>	30.250	-119.750	19.8	22.1
	<i>Formica pallidefulva</i>	24.583	-112.917	24.9	22.1
	<i>Lasius alienus</i>	28.750	-126.583	21.5	12.5
	<i>Lasius flavus</i>	31.917	-123.250	17.7	25.3
	<i>Lasius neoniger</i>	30.583	-126.583	19.5	14.5
	<i>Lasius subglaber</i>	35.417	-111.250	15.6	36.4
	<i>Nylanderia faisonensis</i>	24.583	-95.583	24.9	87.6
	<i>Nylanderia vividula</i>	26.250	-121.750	23.2	14.5
	<i>Prenolepis imparis</i>	28.583	-124.250	22	23.9
Myrmicinae	<i>Aphaenogaster carolinensis</i>	27.250	-109.250	22.3	25.7
	<i>Aphaenogaster fulva</i>	28.583	-105.250	22	40.9

**Table 2** (continued)

Subfamily	Species	Minimum latitude	Minimum longitude	Maximum temperature (°C)	Minimum precipitation (mm)
	<i>Aphaenogaster lamellidens</i>	27.250	-94.250	22.8	91.9
	<i>Aphaenogaster miamiana</i>	25.417	-83.750	24.2	129.2
	<i>Aphaenogaster rudis</i>	24.583	-105.250	24.9	40.9
	<i>Aphaenogaster treatae</i>	27.250	-98.750	22.3	71.1
	<i>Crematogaster ashmeadi</i>	24.583	-97.250	24.9	89.8
	<i>Crematogaster cerasi</i>	27.417	-113.417	22.3	25.6
	<i>Crematogaster lineolata</i>	24.583	-105.250	24.9	40.9
	<i>Crematogaster pilosa</i>	27.083	-92.583	22.6	97.3
	<i>Crematogaster vermiculata</i>	27.917	-118.250	22.3	40.2
	<i>Monomorium minimum</i>	26.250	-119.750	22.7	11.2
	<i>Myrmecina americana</i>	24.583	-122.083	24.9	29.2
	<i>Myrmica punctiventris</i>	30.583	-96.083	19.3	73.8
	<i>Pheidole bicarinata</i>	27.750	-122.917	22.1	13.4
	<i>Pheidole dentata</i>	24.583	-113.417	24.9	22.4
	<i>Pheidole tysoni</i>	29.750	-111.917	20.3	48.9
	<i>Pyramica ornata</i>	27.250	-100.083	22.4	64.7
	<i>Solenopsis molesta</i>	24.583	-126.583	24.9	7
	<i>Strumigenys louisianae</i>	8.583	-103.583	26.3	35
	<i>Temnothorax curvispinosus</i>	30.250	-104.083	19.6	38.6
	<i>Temnothorax longispinosus</i>	30.750	-96.417	19.1	54.4
	<i>Temnothorax pergandei</i>	20.250	-113.250	22.4	25.6
	<i>Temnothorax texanus</i>	27.250	-106.250	22.3	39.7
	<i>Temnothorax tuscaloosae</i>	33.083	-87.583	17	142.7
	<i>Trachymyrmex septentrionalis</i>	24.583	-103.750	24.9	29.4
Ponerinae	<i>Hypoponera opacior</i>	8.417	-149.083	26.4	11.2
	<i>Ponera pennsylvanica</i>	24.583	-108.417	24.9	35

Appendix 2

Table 3 Presence / absence matrix for all sites categorized by land-use types. A=Agriculture, B=Business, \* = non-native species

Subfamily	Species	Agriculture										Business									
		A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10
Amblyoponinae	<i>Amblyopone pallipes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Dolichoderinae	<i>Dorymyrmex bureni</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Forelius pruinosus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Linepithema humile*</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	
	<i>Tapinoma sessile</i>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	
Ecitoninae	<i>Neivamyrmex texanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Formicinae	<i>Brachymyrmex depilis</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	
	<i>Brachymyrmex patagonicus*</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Camponotus americanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Camponotus castaneus</i>	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	0	0	
	<i>Camponotus chromatodes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Camponotus nearcticus</i>	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	
	<i>Camponotus pennsylvanicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Formica dolosa</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	
	<i>Formica subsericea</i>	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	1	0	0	0	
	<i>Formica pallidefulva</i>	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	0	0	0	
	<i>Lasius alienus</i>	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	
	<i>Lasius flavus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Lasius neoniger</i>	1	1	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0	1	1	
	<i>Lasius subglaber</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Nylanderia faisonensis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Nylanderia vividula</i>	1	0	0	1	0	1	1	0	1	1	1	0	1	1	1	1	0	1	1	





Table 3 (continued)

Subfamily	Species	Agriculture										Business									
		A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10
Ponerinae	<i>Hypoponera opacior</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Brachyponera chinensis*</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
	<i>Ponera pennsylvanica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

**Table 4** Presence / absence matrix for all sites categorized by land-use types. G=Greenway, I=Industrial, P=Park, \* = non-native species

Subfamily	Species	Greenway										Industrial										Park									
		G1	G2	G3	G4	G5	G6	G7	G8	G10	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	
Amblyoponinae	<i>Amblyopone pallipes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Dolichoderinae	<i>Dorymyrmex bureni</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Forelius pruinosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	
	<i>Linepithema humile*</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Tapinoma sessile</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	0	
Ecitoninae	<i>Neivamyrmex texanus</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Formicidae	<i>Brachymyrmex depilis</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
	<i>Brachymyrmex patagonicus*</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Camponotus americanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	
	<i>Camponotus castaneus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	
	<i>Camponotus chronaioides</i>	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
	<i>Camponotus nearcticus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Camponotus pennsylvanicus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	
	<i>Formica dolosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Formica subsericea</i>	0	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	1	
	<i>Formica pallidefulva</i>	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
	<i>Lasius alienus</i>	1	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	
	<i>Lasius flavus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Lasius neoniger</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Lasius subglaber</i>	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
	<i>Nyländeria faisonensis</i>	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	
	<i>Nyländeria vividula</i>	0	0	0	1	0	0	0	1	1	0	0	1	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	

**Table 4** (continued)

Subfamily	Species	Greenway										Industrial										Park									
		G1	G2	G3	G4	G5	G6	G7	G8	G10	I1	I2	I3	I4	I5	I6	I7	I8	I9	I10	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	
Myrmicinae	<i>Prenolepis imparis</i>	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	
	<i>Aphaenogaster carolinensis</i>	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	
	<i>Aphaenogaster fulva</i>	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0	0	
	<i>Aphaenogaster lamellidens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
	<i>Aphaenogaster miamiana</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Aphaenogaster rudis</i>	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
	<i>Aphaenogaster treatae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
	<i>Crematogaster ashmeadi</i>	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	
	<i>Crematogaster cerasi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Crematogaster lineolata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
	<i>Crematogaster pilosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Crematogaster vermiculata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Monomorium minimum</i>	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	0	0	1	1	1	1	1	1	
	<i>Myrmecina americana</i>	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
<i>Myrmica punctiventris</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Pheidole bicarinata</i>	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1		
<i>Pheidole dentata</i>	0	0	1	1	1	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	1	1	0	0	1	1		
<i>Pheidole tysoni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0		
<i>Pyramica ornata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Solenopsis invicta*</i>	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	1	1	1	0	1	0	1	0	0	0	0	0	1	1		
<i>Solenopsis molesta</i>	1	0	1	1	0	1	1	1	1	1	0	0	0	0	1	0	1	0	1	1	0	1	0	1	0	1	1	1	0		
<i>Strumigenys louisianae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		



**Table 5** Presence / absence matrix for all sites categorized by land-use types. R=Residential, \*=non-native species

Subfamily	Species	Residential																															
		R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	R11	R12	R13	R14	R15	R16	R17	R18	R19	R20	R21	R22	R23	R24	R25	R26	R27	R28	R29	R30		
Amblyoponinae	<i>Amblyopone pallipes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Dolichoderinae	<i>Dorymyrmex bureni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>Forelius pratensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0		
	<i>Linepithema humile*</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>Tapinoma sessile</i>	0	1	0	1	0	1	1	0	0	1	0	0	1	0	0	1	1	0	1	0	1	1	1	1	0	0	1	0	1	1		
Ectoninae	<i>Neivamyrmex texanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Formicinae	<i>Brachymyrmex depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>Brachymyrmex patagonicus*</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>Camponotus americanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
	<i>Camponotus castaneus</i>	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	
	<i>Camponotus chromitoides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Camponotus nearcticus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Camponotus pennsylvanicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Formica dolosa</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Formica subsericea</i>	1	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	
	<i>Formica pallidefulva</i>	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Lasius alienus</i>	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	
	<i>Lasius flavus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Lasius neoniger</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Lasius subglaber</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<i>Nylanderia faisonensis</i>	1	0	0	0	1	0	0	0	1	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0
	<i>Nylanderia vividula</i>	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0
	<i>Prenolepis imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myrmicinae	<i>Aphaenogaster carolinensis</i>	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0	1	0	0



**Table 6** Presence / absence matrix for all sites categorized by land-use types. F=Forest, \*=non-native species

Subfamily	Species	Forest												
		F1	F2	F3	F5	F7	F14	F16	F18	F20	F21			
Amblyoponinae	<i>Amblyopone pallipes</i>	0	0	0	1	0	0	0	0	0	0	0	0	0
Dolichoderinae	<i>Dorymyrmex bureni</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Forelius pruinosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Linepithema humile*</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Tapinoma sessile</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
Ecitoninae	<i>Neivamyrmex texanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
Formicinae	<i>Brachymyrmex depilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Brachymyrmex patagonicus*</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Camponotus americanus</i>	0	0	0	1	1	0	0	0	0	0	0	0	0
	<i>Camponotus castaneus</i>	1	0	1	1	1	1	0	1	1	0	1	1	0
	<i>Camponotus chromaiodes</i>	0	0	0	0	0	1	0	1	0	0	1	0	1
	<i>Camponotus nearcticus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Camponotus pennsylvanicus</i>	1	0	0	1	1	0	0	0	0	0	0	1	1
	<i>Formica dolosa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Formica subsericea</i>	0	0	1	1	1	1	1	1	1	1	1	0	0
	<i>Formica pallidefulva</i>	0	0	0	0	0	0	0	1	0	0	1	0	1
	<i>Lasius alienus</i>	1	1	0	0	0	0	0	1	0	0	0	0	1
	<i>Lasius flavus</i>	0	1	0	1	1	0	0	0	0	0	0	0	0
	<i>Lasius neoniger</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Lasius subglaber</i>	1	0	0	0	0	0	0	0	0	0	0	0	0
	<i>Nylanderia faisonensis</i>	1	1	0	1	0	1	1	1	0	0	0	0	0
	<i>Nylanderia vividula</i>	0	0	0	1	0	1	0	0	0	0	0	0	0
	<i>Prenolepis imparis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0





Table 6 (continued)

Subfamily	Species	Forest										
		F1	F2	F3	F5	F7	F14	F16	F18	F20	F21	
Ponerinae	<i>Hypoponera opacior</i>	0	0	0	0	0	0	0	0	0	0	1
	<i>Brachyponera chinensis</i> *	1	0	0	0	1	1	0	0	1	1	1
	<i>Ponera pennsylvanica</i>	0	1	1	0	0	0	0	0	1	1	0

### Appendix 3

**Table 7** Comparison of all possible pair-wise combinations of land-use types with MRPP, based on Sorensen distances. A=chance-corrected between-group agreement; p=probability of Type I error for no difference between groups. Significant p-value after Bonferonni correction=0.00238

Group	T statistic	A	p
Agriculture vs. Business	-1.87	0.03	0.05
Agriculture vs. Greenway	-7.38	0.02	< 0.001
Agriculture vs. Industrial	-1.99	0.04	0.05
Agriculture vs. Park	-3.46	0.05	0.01
Agriculture vs. Residential	-7.18	0.05	< 0.001
Agriculture vs. Forest	-10.59	0.23	< 0.001
Business vs. Greenway	-7.450	0.12	< 0.001
Business vs. Industrial	-0.12	0	0.37
Business vs. Park	-1.71	0.02	0.060
Business vs. Residential	-2.28	0.02	0.03
Business vs. Forest	-10.57	0.18	< 0.001
Greenway vs. Industrial	-6.99	0.13	< 0.001
Greenway vs. Park	-1.73	0.03	0.06
Greenway vs. Residential	-7.49	0.05	< 0.001
Greenway vs. Forest	-8.71	0.14	< 0.001
Industrial vs. Park	-2.32	0.03	0.03
Industrial vs. Residential	-2.88	0.02	0.02
Industrial vs. Forest	-10.15	0.18	< 0.001
Park vs. Residential	-2.710	0.02	0.01
Park vs. Forest	-8.19	0.11	< 0.001
Residential vs. Forest	-15.5	0.11	< 0.001

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